FLOW DIAGRAMS FOR PLANT SUCCESSION IN THE MIDDLE TENNESSEE CEDAR GLADES

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ABSTRACT

Elsie Quarterman's comprehensive study of cedar glade vegetation in the Inner Central (Nashville) Basin of Tennessee did not include flow diagrams for any of the multiple pathways of succession she described in her Ph.D. thesis (Quarterman 1948) or in her major publication on cedar glades (Quarterman 1950a). Thus, our primary objective was to construct conceptual models (flow diagrams) for the various (inferred) successional pathways from bare limestone bedrock to subclimax redcedar, preclimax oak-hickory and mixed hardwood forests, based primarily on Quarterman's study. A second objective was to discuss how other quantitative studies on cedar glade vegetation in the Inner Basin fit into Quarterman's schemes. These diagrams, along with how other studies correlate with them, will make it easier to interpret the interrelationships of the various plant communities (vegetation zones) in the middle Tennessee cedar glade vegetation complex and thus be an aid to conservation planning in the Nashville Basin.

ABSTRACT

El estudio exhaustivo de Elsie Quarterman de la vegetación de los "cedar glades" en la cuenca interior central (Nashville) de Tennessee no incluyó diagramas de flujo de ninguna de las múltiples vías de sucesión que describió en su tesis (Quarterman 1948) o en su publicación más importante sobre los "cedar glades" (Quarterman 1950a). Así pues, nuestro objetivo primario fue construir modelos conceptuales (diagramas de flujo) de las varias (inferidas) vías de sucesión desde la caliza desnuda a la subclímax de cedro rojo, preclímax roble-nogal y bosques mixtos de madera dura, basados principalmente en el estudio de Quarterman. Un segundo objetivo fue discutir como otros estudios cuantitativos sobre vegetación de los "cedar glade" de la cuenca interior concuerdan con los esquemas de Quarterman. Estos diagramas, junto con las correlaciones con otros estudios, harán más fácil la interpretación de las interrelaciones de las diferentes comunidades vegetales (zonas de vegetación) en el complejo de vegetación de "cedar glade" de Tennessee central y de este modo ser una ayuda en la planificación de la conservación en la cuenca de Nashville.

INTRODUCTION

The Inner Central (Nashville) Basin is well known for its cedar glade vegetation (e.g., Harper 1926; Freeman 1933; Quarterman 1950 a, b; Kuchler 1964; Baskin & Baskin 2004). Historically, in the Central Basin the term "cedar glades" (sensu lato) has been used to include both the natural rocky limestone openings ("glades") and the adjacent redcedar-redcedar/hardwood forest complex, and Galloway (1919) even recognized "massive rock or hardwood glades" (Baskin & Baskin 2004). More recently, however, botanists have used "cedar glades" (sensu stricto) in reference to the rocky openings only, i.e., "glades" or "open glades" sensu Quarterman (Baskin & Baskin 2004). Thus, cedar or limestone glades in the Inner Basin are open areas of rock pavement, gravel, flagstone and/or shallow soil in which occur natural, long-persisting (edaphic climax) plant communities dominated by herbaceous angiosperms and/or cryptogams (Baskin & Baskin 1985; Quarterman et al. 1993; Ware 2002). They may, or may not, be surrounded by forest (Galloway 1919). Cedar glades may support low densities of woody plants, which become established in deep soil-filled cracks in the bedrock [e.g., Picklesimer (1927; see Fig. 1 in Baskin & Baskin 1996a); Quarterman 1950a]. The dominant plants are C_4 summer annual grasses (primarily *Sporobolus vaginiflorus* but also *Panicum capillare* and *P. flexile*); C_3 winter annual, summer annual and/or perennial herbaceous dicots; mosses (primarily *Pleurochaete squarrosa*); the cyanobacterium *Nostoc commune*; and crustose, foliose and fruticose lichens [Picklesimer (1927; see Baskin & Baskin 1996a); Freeman 1933; Quarterman 1950a,b; Somers et al. 1986; Mahr & Mathis 1981; Dubois 1993; Baskin & Baskin 1996b; Rollins 1997].

The most complete, comprehensive study of cedar glade vegetation in the Central Basin (as well as in the southeastern USA in general) was done by Elsie Quarterman (1948, 1950a, b). She described (apparent) successional pathways that theoretically represent the various stages in vegetation development from bare rock to oak-hickory forest or to a subclimax redcedar (*Juniperus virginiana*) forest. Quarterman determined constancy of plant species in 22 open glades and in 10 glade woods in the Inner Basin (sensu Edwards et al. 1974; also see DeSelm 1959), and she used quadrats to sample intensively the following stages in the (apparent) successional sequence of plant communities: gravel glade, grass glade, glade-shrub, shrub-cedar, 88-year-old cedar forest, 103-year-old cedar forest and cedar-hardwood forest. She referred to gravel and grass glades, along with rock glades, which she did not quantitatively sample, as open glades. These open glades are the "cedar glades" sensu stricto defined above.

Although Quarterman described succession from bare rock to redcedar and redcedar/hardwood forests in considerable detail, she did not conceptualize, via flow diagrams, the various pathways and their relationship to each other. Since Quarterman's (1950a) classic publication, two flow diagrams of vegetation development in the cedar glades of the Central Basin have been published (Quarterman et al. 1993; Baskin & Baskin 2004). However, neither of these diagrams shows the complexity of successional pathways that lead from bare rock to redcedar and hardwood forests (Quarterman 1950a). Thus, our objectives were to (1) construct detailed diagrams showing vegetation development in the cedar glades (sensu lato) of the Central Basin of Tennessee, based primarily on Quarterman (1948, 1950a), and (2) discuss how other quantitative studies on cedar glade vegetation in the Inner Nashville Basin fit into Quarterman's schemes. The initial work on constructing these diagrams began when Jerry and Carol Baskin were graduate students at Vanderbilt University in the 1960s and were beginning to learn about the middle Tennessee cedar glades from Professor Elsie Quarterman. Although the primary sources for the successional pathways and seral stages is Quarterman (1948, 1950a), other sources include Picklesimer (1927; see Baskin & Baskin, 1996a), Freeman (1933), McKinney & Hemmerly (1984), Crites and Clebsch (1986), Somers et al. (1986), DeSelm (1989, 1992), Baskin and Baskin (1996b), Rollins (1997) and numerous unpublished observations by Jerry and Carol Baskin in the middle Tennessee cedar glades. Nomenclature primarily follows that used by Baskin and Baskin (2003).

SUCCESIONAL PATHWAYS

In actuality, Quarterman's presumed successional pathways may represent vegetational sequences along xeric to submesic environmental gradients that are unrelated to succession. In any case, whether the vegetation mosaic represents seral stages or vegetation zones unrelated to succession, the cedar glades support a complex of plant groupings ("associations") that are difficult to comprehend via written descriptions, even when the text is supplemented with photographs and a considerable amount of data on community composition and structure, as is the case with Quarterman's study. Thus, thinking of these various communities in a successional or developmental context helps to clarify the structural relationships among them.

Limestone without cracks

Primary succession on limestone without cracks is shown in Figure 1. There are two starting points: one in slight depressions (with small amounts of mineral soil and gravel) on bare rock pavement of thick beds primarily of the Middle Ordovician Ridley (Ord) and Lebanon (Olb), but also on Pierce and Murfreesboro (Opm, mapped as a unit) (*e.g.* Ware 1969; Baskin and Quarterman 1970) limestones, and the other on flagstone/gravel glades weathered from thin beds of the Lebanon [see photographs (Fig. 12.1) in Baskin & Baskin 1999], on which most of the cedar glades in the Central Basin have developed (Safford 1851; see Baskin &

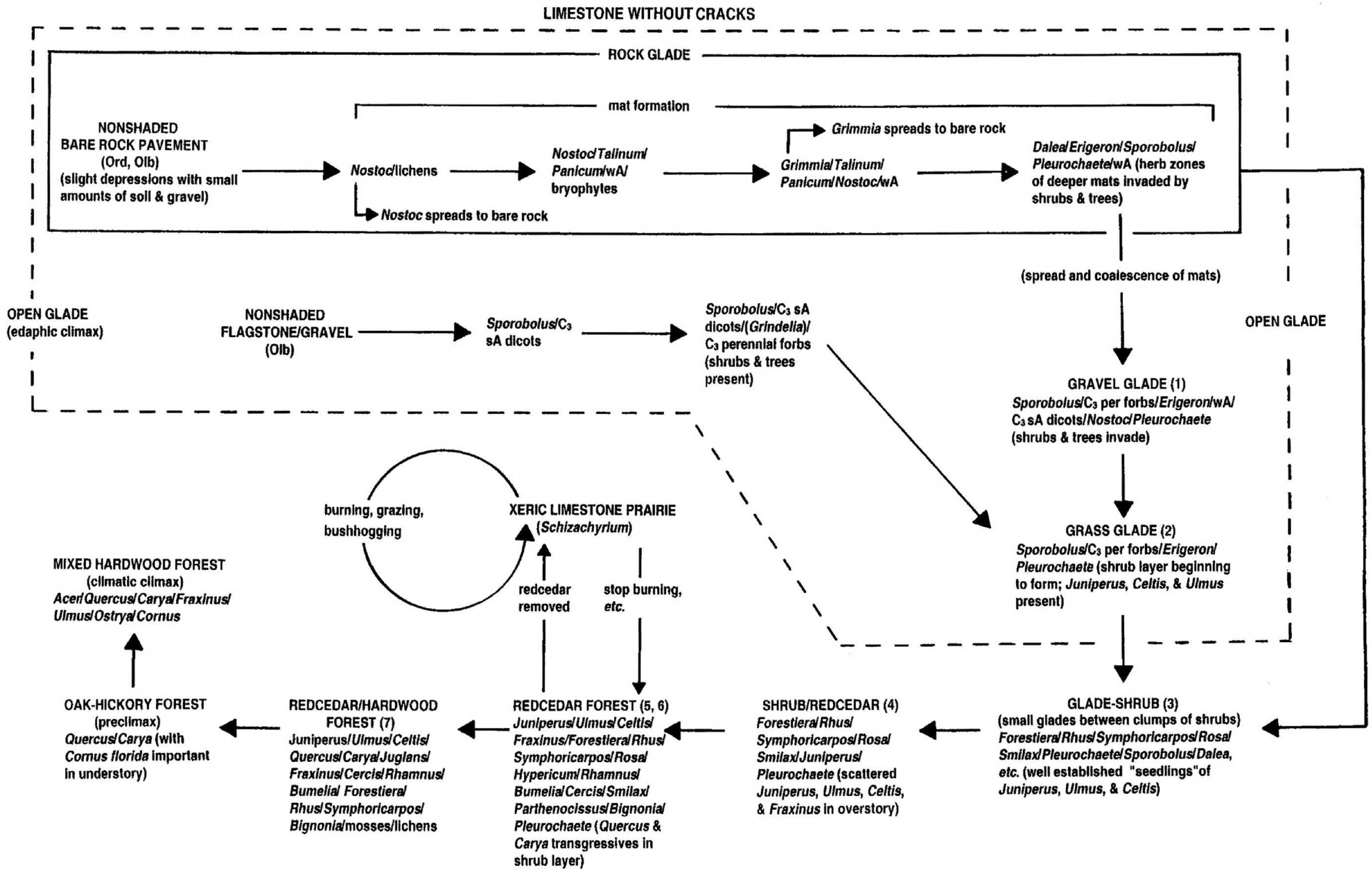

Fig. 1. Inferred pathways of plant succession on thick-bedded limestone without cracks and on thin-bedded (flagstone/gravel) limestone in the cedar glades of middle Tennessee. Olb, Middle Ordovician Lebanon limestone; Ord, Middle Ordovician Ridley limestone; sA, summer annuals, e.g., Cyperus squarrosus (= C. aristatus, C. inflexus)(C_4), Heliotropium tenellum, Isanthus brachiatus (C_3), Panicum capillare and P. flexile (C_4); wA, winter annuals, e.g. Arenaria (Minuartia) patula, Leavenworthia spp., Sedum pulchellum; per, perennial, e.g. Dalea gattingeri, Hypericum sphaerocarpum and Pediomelum subacaule. Successional stages quantitatively sampled by Quarterman (1948, 1950a) are shown by numbers (1–7). The redcedar forest successional stage (5, 6) represents a combination of Quarterman's (1948, 1950a) 88-year-old and 103-year-old redcedar forest stands. The oak-hickory preclimax forest is based on stand number 5 (on Ord) of McKinney and Hemmerly (1984).

Baskin 2004). No mats form directly on the rock surface, although *Nostoc commune* and *Grimmia apocarpa* may spread to bare rock. Mats of herbaceous vegetation formed during succession on rock glades coalesce into gravel glades. Then, further on in the sequence, the two pathways of succession join to form the grass-glade stage, which is followed by the glade-shrub, shrub-redcedar, redcedar forest and redcedar-hardwood forest seral stages, and finally by an oak-hickory preclimax forest. The last stage of mat formation (rock glades) may proceed directly to the glade-shrub stage, when woody plants become established in deeper parts of the mat and/or vertical crevices in the bedrock, thus by-passing the gravel and grass stages.

Also shown in Figure 1 is the relationship between the redcedar forest stage of succession and the formation of rock barrens (sensu DeSelm 1992; = xeric limestone prairies sensu Baskin et al. 1994; Baskin & Baskin 2000, 2004; Lawless et al. 2006 [see photographs (Fig. 3) in Baskin & Baskin 2004]. According to DeSelm (1992), "Environmentally and vegetationally these barrens 'fit' between cedar glades and cedar or oak forests with deeper soil." Further, "Barrens in the Basin occur on the soil thickness/available moisture gradient between cedar glades and cedar forests. Today, they probably occur chiefly on sites where the cedar has been removed. Maintenance of such openings against cedar and hardwood successional pressure has been accomplished by grazing, fire and today perhaps by bushhogging."

Limestone with vertical cracks

The multiple pathways on limestone with vertical cracks, as discussed by Quarterman (1950a), are diagrammed in Figure 2. In cracks that are widely-spaced and parallel to each other, succession leads to an open glade with lines of trees and shrubs. Between the cracks, the successional sequence is similar to that shown in Figure 1, i.e., from the gravel glade stage to the grass glade stage and on to oak-hickory forest.

In cracks that are close together and intersecting, the successional sequence is from herbs to shrubs to redcedar. In the redcedar forest, a moss mat forms on small ledges and sides of cracks in the bedrock, which is invaded by herbs, ferns and lichens. On large flat blocks of limestone between cracks in the redcedar forest, succession in partial shade begins with the moss *Orthotrichum strangulatum* or the cyanobacterium *Nostoc commune* and then proceeds to the moss *Pleurochaete squarrosa*, which may be long-persisting, to herbs and finally to shrubs. On flat blocks of limestone in shade, succession begins with *Orthotrichum strangulatum* and ends with a *Climacium americanum* (moss)-fern-herb stage. These four successional pathways in areas with cracks that are close together and intersecting result in a redcedar subclimax forest with shrub, moss and fern-herb layers beneath the canopy of *Juniperus virginiana* trees.

The bark of redcedar trees forms a substrate for establishment of corticolous bryophytes, the mats of which may also include species of cyanobacteria, fungi and lichens (Quarterman 1949). A successional sequence begins on the smooth bark of young (single, unshaded) redcedar tree trunks with the mosses *Frullania* and *Orthotrichum*, proceeds to a *Leucodon-Cryphaea-Chasmatodon* stage (woods margin, generally older trees than in first stage) and then to a *Leucodon-Porella* (leafy liverwort) stage (on older trees within redcedar forests). *Porella* (only on trees in forest) sometimes forms pure colonies, which may be invaded by the fern *Polypodium polypodioides* (Quarterman 1949). Thus, in general, the majority of moss mats on young redcedar trees represents early stages of succession and the majority of those on old redcedar trees later stages of succession. However, new surfaces created by the shedding of bark, even on old trees, are invaded by the same pioneers (Fig. 2, in REDCEDAR SUBCLIMAX) that occur on young trees, providing "…evidence that a rather definite scheme of succession occurs on bark of cedar trees" (Quarterman 1949).

QUARTERMAN'S SCHEMES IN RELATION TO OTHER STUDIES

Picklesimer (1927; see Baskin and Baskin 1996a) counted all individuals along a 404 ft (123 m) × 1 ft (0.3 m) transect in a open glade apparently on a thick-bed (see her Fig. 4) of the Lebanon limestone (Inner Basin). The transect was divided into 21 zones: 16 in open glades and five in glade woods. Forty-seven percent of the 42,207 individuals recorded along a transect by Picklesimer in the open glade were plants of *Sedum pulchellum*, and 30.4% were plants of *Arenaria* (*Minuartia*) *patula*. *Sedum* was the most abundant plant in eight of 16 open glade zones and *Arenaria* in five. *Panicum capillare*, *Sporobolus vaginiflorus* and

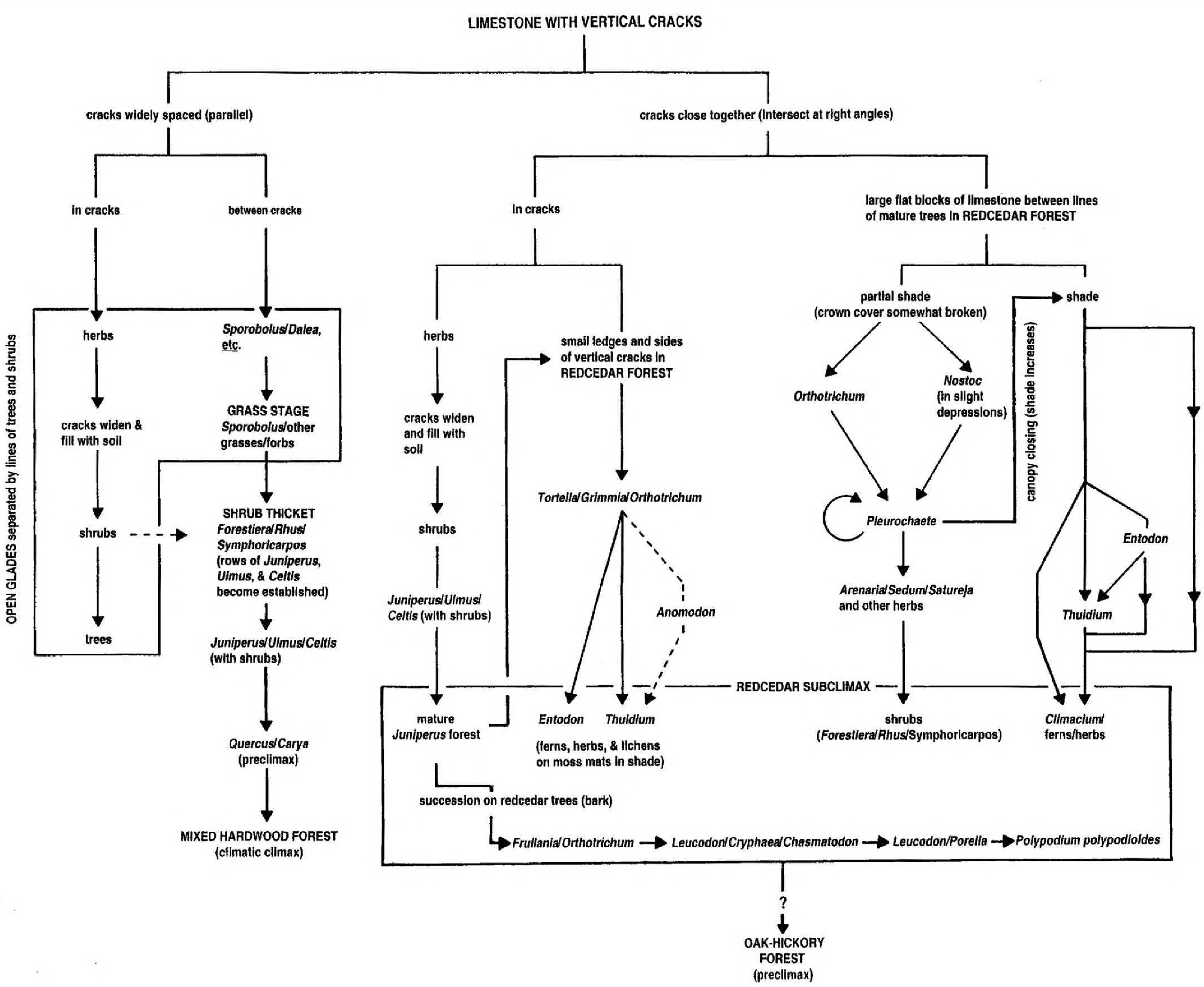

Fig. 2. Inferred pathways of plant succession on limestone with vertical cracks in the cedar glades of middle Tennessee. The dashed line from Tortella/ Grimmia/Orthotrichum through Anomodon to Thuidum indicates that this pathway is occasional.

Erigeron strigosus [= *E. strigosus* Muhl. ex Willd. var. *calcicola* J. Allison (Allison and Stevens 2001; Noyes and Allison, 2005)] ranked third, fourth and fifth, respectively, in order of abundance. Plants of each of the cedar glade endemics *Leavenworthia torulosa*, *Lobelia appendiculata* var. *gattingeri*, *Phacelia dubia* var. *interior* and *Talinum calcaricum* were present in several of the zones. Redcedar (*Juniperus virginiana*) was by far the dominant tree in the glade woods with *Adelia* (*Forestiera*) *ligustrina* (shrub), *Ulmus alata* and *Celtis mississippiensis* (= *C. laevigata*) second, third and fourth, respectively, in abundance. The vegetation of the open glade sampled by Picklesimer fits primarily in the rock glade category (Fig. 1) and that of the glade woods in the redcedar forest (*Juniperus/Ulmus/Celtis/Forestiera*) (Fig. 1, 2; see Fig. 1, 2 in Baskin & Baskin 1996a). Picklesimer proposed that the successional pathway in cedar glades begins with crustose lichens (pioneers) and ends with a redcedar climax forest. See Baskin and Baskin (1996a) for updating of nomenclature used by Picklesimer (1927).

Freeman (1933) used 1 ft^2 (0.09 m^2) quadrats to determine the relative abundance of species in five spring and 10 summer aspect societies in an open glade in Davidson County, Tennessee, near LaVergne (Inner Basin). The 15 aspect societies were (1) *Dalea gattingeri* (not *D. foliosa* as indicated by Freeman, i.e., see his figure 18, which is a photograph of *D. gattingeri* and not *D. foliosa*)-*Sporobolus vaginiflorus*; (2) *Hypericum sphaerocarpum-Dalea gattingeri*; (3) *Croton monanthogynus-Cocculus carolinus*; (4) *Isanthus brachiatus-Hypericum sphaerocarpum*; (5) *Croton capitatus*; (6) *Croton monanthogynus*; (7) *Erigeron strigosus-Lespedeza striata* (not native); (8) *Diodia teres-Croton capitatus*; (9) *Hypericum sphaerocarpum*; (10) *Sedum pulchellum*; (11) *Arenaria patula*; (12)

Leavenworthia stylosa; (13) *Leavenworthia stylosa-Ophioglossum engelmannii*; (14) *Delphinium carolinianum* [= D. *carolinianum* Walter subsp. *calciphilum* Warnock; Warnock (1990, 1997)]; and (15) *Isoetes butleri*. However, we do not consider the *Croton monanthogynus-Cocculus carolinus* or the *Erigeron strigosus-Lespedeza striata* societies to have been on open cedar glades since the soil was up to 61 cm deep (see Baskin & Baskin 2004).

Overall, species with the highest % importance values (% IVs) [(relative frequency + relative density)/2] × 100 calculated from Freeman's data on frequency and density of taxa in the 13 societies on open cedar glades were (in decreasing order): *Minuartia patula*, *Sporobolus vaginiflorus*, *Sedum pulchellum*, *Leavenworthia stylosa*, *Hypericum sphaerocarpum*, *Croton capitatus*, *Isoetes butleri*, *Dalea gattingeri*, *Croton monthogynus*, *Isanthus brachiatus* and *Panicum capillare*. *Sporobolus vaginiflorus* ranked first in the *D. gattingeri-S. vaginiflorus*; *H. sphaerocarpum-D. gattingeri*; *I. brachiatus-H. sphaerocarpum*; *C. monthogynus*; *D. teres-C. capitatus;* and *H. sphaerocarpum-S. pulchellum* societies and second in the *C. capitatus* society. This species was not present in the *Sedum*, *Arenaria*, *L. stylosa* or *L. stylosa-O. engelmannii* societies. Except for *D. carolinianum* and *I. butleri*, no data on species composition/abundance are given for these two societies. Seemingly, the seven societies in which *S. vaginiflorus* is important represent gravel and/or grassy glades, while the *S. pulchellum*, *A. patula*, *L. stylosa* and *L. stylosa-O. engelmannii* societies belong to rock glades (Fig. 1, 2).

In a study of the ecological distribution of *Talinum calcaricum* on rock (Opm) glades near Murfreesboro, Tennessee (Inner Basin), Ware (1969) recognized four vegetation zones in the "ecotone" between bare rock and grass-dominated glades (0–10 cm soil depth): *Nostoc-Talinum; Sedum-Nostoc-Talinum; Arenaria-Talinum*-moss; and *Pleurochaete* (moss)-*Talinum*. Ware's first and second zones appear to correspond to the *Nostoc/Talinum/Panicum/* wA/ bryophyte and *Grimmia/Talinum/Panicum/Nostoc*/wA zones, respectively, and his third and fourth zones to the *Dalea/Erigeron/Sporobolus/Pleurochaeta*/wA zone (Fig. 1). He did not include a *Nostoc*/lichens zone (Fig. 1) in the ecotone between bare rock and grass-dominated glades.

Later on in her career, Quarterman (1973, 1989, 1993) recognized two characteristic zones or communities of open cedar glades in the Inner Central Basin: Zone I (soil depth 0–5 cm; = gravel glades of Quarterman et al. 1993); and Zone II (soil depth ca. 5–20 cm; = grassy glades of Quarterman et al. 1993). The shallow portions of Zone I are dominated by the winter annuals *Minuartia patula*, *Leavenworthia* spp. and *Sedum pulchellum*; and in summer by the summer annuals *Cyperus squarrosus* (= *C. aristatus*, *C. inflexus*) and the small succulent polycarpic perennial *Talinum calcaricum*. *Nostoc commune* grows on bare rock. In deeper soil of this zone, the dominant plants are the long-lived polycarpic perennial *Dalea gattingeri*, the biennial *Erigeron stigosus* and the moss *Pleurochaete squarrosa*. Zone II is dominated by the C_4 summer annual grasses *S. vaginiflorus*, *Panicum capillare* and *Aristida longespica* (occasional) and the moss *P. squarrosa*; many other species occur in this zone.

Somers et al. (1986) quantitatively sampled 10 open glades in the Inner Central Basin and identified four xeric (soil < 5 cm deep) - *Panicum capillare*; foliose lichens, *Nostoc commune-Sporobolus vaginiflorus* and *Dalea gattingeri*; and three subxeric (soil > 5 cm deep) - *Sporobolus vaginiflorus, Pleurochaete squarrosa* and *Panicum flexile-Pleurochaete squarrosa-S. vaginiflorus* plant communities. Quarterman's zones I and II, which she equated with rock-gravel glades and grassy glades, respectively (Quarterman et al. 1993), correspond closely to Somers et al.'s xeric and subxeric plant communities, respectively (Somers et al. 1986; Quarterman et al. 1989).

Using combined plot data from five sites on open cedar glades in the Inner Basin that supported populations of the federally –endangered species *Echinacea tennesseensis,*Drew (1991; also see Drew and Clebsch 1995) identified six plant communities: *Echinacea/Ruellia*; *Houstonia/ Sporobolus*; *Sporobolus/Petalostemon* (*Dalea*); *Echinacea*; *Schizachyrium/ Houstonia*; and *Echinacea/Schizachyrium.* These community types differ somewhat from the vegetation zones (community types) recognized by Quarterman (1950a) and also from those recognized by Somers et al. (1986) and Rollins (1997). Thus, for example, whereas *Echinacea tennesseensis* and/or *Schizachyrium* are important components of four of Drew's across-site community types, neither species was present in any of the vegetation zones of open cedar glades recognized by Quarterman (Fig. 1, 2).

On the other hand, % importance values (% IVs) [(relative cover + relative frequency)/2] × 100 calculated for taxa at each of the five glade sites sampled by Drew showed that *Sporobolus vaginiflorus* had the highest average across-site % IV. Other important plants of open Lebanon limestone glades in Drew's study included *Hedyotis nigricans*, *Ruellia humilis*, *Grindelia lanceolata*, *Dalea gattingeri*, *Hypericum sphaerocarpum* and *Isanthus brachiatus* (Fig. 1, 2). Further, as pointed out by Baskin and Baskin (2004), Drew misinterpreted Quarterman's and Hal DeSelm's (see Quarterman 1989; Quarterman et al. 1993; DeSelm 1992) definition of glades (<50% perennial grass cover) and barrens (≥ 50% perennial grass cover), and as a result he assigned two of his six community types to barrens, based on 19% and 15% cover of the (only) perennial grass, *Schizachyrium scoparium,* in the two community types. However, using the criteria of Quarterman and DeSelm for glades *vs*. barrens, all five open glade sites quantitatively sampled by Drew (1991; Drew and Clebsch 1995) are subxeric open cedar glades.

Baskin and Baskin (1996b) described a *Grindelia lanceolata* plant community type on the (mostly) thin-bedded Lebanon limestone about 7.0 km north of LaVergne (Rutherford County) in the Inner Basin. *Grindelia lanceolata* (100% frequency), *Sporobolus vaginiflorus* (96.5%) and *Dalea gattingeri* (91.8%) had the highest frequencies of the 51 native and 3 nonnative species present in 85 1-m^2 sample plots. This community and NatureServe's (2005) *Sporobolus* (*neglectus*, *vaginiflorus*)-*Aristida longespica*-*Panicum flexile*-*Panicum capillare* Herbaceous Vegetation Association of the *Sporobolus* (*neglectus*, *vaginiflorus*) Herbaceous Alliance fit the subxeric portion of the open glades category described by Quarterman (Fig. 1, 2).

Rollins (1997) sampled 10 open glades in the Inner Central Basin and delineated 10 community types at the 10-m^2 scale and 14 at the 0.1-m^2 scale. She assigned names to them based on the two to six and two to four most important species, respectively, in order of decreasing cover and constancy. Species included in names of 10 community types identified, with the total number of times that species is used (base number) and number of times it ranked 1, 2, 3, 4, 5 and/or 6 (10-m^2 scale) or 1, 2, 3 and/or 4 (0.1-m^2 scale) (exponents of base number) are as follows: for communities identified at the 10-m^2 scale – *Sporobolus vaginiflorus*, $10^{(6,4)}$, *Dalea gattingeri* $5^{(0, 1, 3, 1)}$, *Pleurochaeta squarrosa* $6^{(4, 2)}$, *Andropogon virginicus* $4^{(0, 2, 1, 1)}$, *Nothoscordum bivalve* $2^{(0, 0, 2)}$, *Grindelia lanceolata* var. *lanceolata* $2^{(0, 0, 0, 2)}$, *Hedyotis nigricans* var. *nigricans* $2^{(0, 0, 0, 1, 1)}$, *Eleocharis compressa* $1^{(0, 1)}$, *Carex crawei* $1^{(0, 0, 1)}$, *Aristida longespica* $1^{(0, 0, 1)}$, *Pediomelum subacaule* $1^{(0, 0, 0, 1)}$, *Ruellia humilis* $1^{(0, 0, 0, 0, 1)}$ and *Senecio anonymous* $1^{(0, 0, 0, 0, 0, 1)}$; and for communities identified at the 0.1-m^2 scale - *Sporobolus vaginiflorus*, $10^{(2, 6, 2)}$, *Dalea gattingeri* $4^{(1, 2, 1)}$, *Grindelia lanceolata* var. *lanceolata* $3^{(1, 1, 0, 1)}$, *Nothoscordum bivalve* $3^{(2, 0, 1)}$, *Nostoc commune* $3^{(0, 2, 1)}$, *Ruellia humilis* $2^{(1, 0, 1)}$, *Hedyotis nigricans* var. *nigricans* $2^{(2)}$, *Sedum pulchellum* $1^{(1)}$, *Carex crawei* $1^{(1)}$, *Ratibida pinnata* $1^{(1)}$, *Eleocharis compressa* $1^{(1)}$, *Andropogon virginicus* $1^{(1)}$, *Pediomelum subacaule* $1^{(0, 1)}$, *Aristida longespica* $1^{(0, 1)}$, *Manfreda virginica* $1^{(0, 1)}$, *Minuartia patula* $1^{(0, 0, 1)}$ and *Calmintha glabella* $1^{(0, 0, 1)}$. Rollins used *Pleurochaete squarrosa* as a substrate type in sampling at the 0.1-m^2 scale, and thus did not include its cover or constancy in her samples, which explains why there are no data for this moss in her community types identified at the 0.1-m^2 scale.

Rollins' community types differ somewhat from those recognized by Quarterman. Thus, whereas *Andropogon virginicus* and wet-loving plants such as *Carex*, *Eleocharis* and *Nothoscordum* (see above) were important components of the open glades sampled by Rollins, they were not important in those sampled by Quarterman (Fig. 1, 2). However, *Sporobolus vaginiflorus*, the overall dominant in open cedar glades of the Central Basin (see Baskin and Baskin 1999), also was the most important species in Rollins' study. Rollins states that her study agrees with those of Quarterman in dividing open cedar glades into xeric (gravel) and subxeric (grassy) zones with "… the only exception being low abundances of *Pleurochaete* and foliose lichens in the 'xeric' zone communities described here."

The overall vegetation of the five forest stands sampled by McKinney and Hemmerly (1984) on Carters and Ridley limestones in the Inner Basin was a mixed hardwood (oak-hickory-maple-ash-elm) forest. However, four of the five stands sampled by these authors were on the thick-bedded Carters Limestone, which overlies the Lebanon and generally is not a glade-forming limestone. Their other stand, which was on the thick-bedded Ridley, a glade-forming limestone, was dominated by *Quercus*-*Carya* (%IV, 67.2). Thus, it is an example of the oak-hickory stage shown in Figures 1 and 2. In the seemingly most mesic stand (number 3) sampled by McKinney and Hemmerly (1984), *Acer saccharum* had the highest % IV (37.9) followed by *Quercus* spp. (32.4), *Carya* spp. (23.2) and *Fraxinus* spp. (17.3), a mixed hardwood forest (Fig. 1,2). The overall upland forest vegetation on Ridley (redcedar-sugar maple-hickory-oak-ash-elm) and Lebanon (redcedar-oak-hickory-ash-elm) limestones in the Inner Basin sampled by Crites and Clebsch (1986) are examples of redcedar/hardwood forests in Figure 1. Seemingly, the most mesic stand sampled by these authors was a *Acer saccharum/Fraxinus americana/Ostrya virginiana* plant community type on Ridley Limestone, another example of mixed hardwood forest in the Inner Basin. NatureServe's (2005) *Juniperus virginiana* var. *virginiana-Forestiera ligustrina-Rhus aromatica-Hypericum frondosum* Shrubland Association of the *Juniperus virginiana-Rhus aromatica* Alliance fits well with the glade-shrub and redcedar stages, and its *Juniperus virginiana* var. *virginiana-Fraxinus quadrangulata/Polymnia canadensis* (*Astranthium integrifolium*) Woodland of the *Fraxinus quadrangulata* –(*Juniperus virginiana*) Woodland Alliance more or less with the redcedar and redcedar/hardwood forests (Fig. 1, 2).

Finally, NatureServe's (2005) *Quercus muehlenbergii-Juniperus virginiana* Wooded Herbaceous Association of the (*Juniperus virginiana/Schizachyrium scoparium-Bouteloua curtipendula*) Wooded Herbaceous Alliance, the little bluestem-dominated glades described by Baskin and Baskin (1977; see Fig. 1 in this paper) and the four barrens on Ridley and Lebanon limestones described by DeSelm (1992) fit what we refer to in Figure 1 as xeric limestone prairies, an anthropogenically-derived plant community.

Not evident from Figure 1 is the fact that successional stages on open glades may be wet enough in spring to support such moisture-loving plants as *Isoetes butleri*, *Carex* species (especially *C. crawei*), *Eleocharis bifida* S. G. Smith [segregated from *E. compressa* (Smith, 2001, 2002)], *Nothoscordum bivalve* and *Schoenolirion croceum*. However, Quarterman (1950b) did mention a group of species that included *Isoetes butleri*, *Nothoscordum bivalve*, *Schoenolieron croceum* and *Leavenworthia* spp, among others, that "…flourishes and blooms in early spring when the ground is saturated." Freeman (1933) recognized an *Isoetes butleri* aspect on open cedar glades, and he commented that, "The area occupied by *Isoetes* was very wet during the early spring." *Carex crawei, Eleocharis compressa* and *Nothoscordum bivalve* were used by Rollins (1997) in naming three of the 10 open cedar glade community types she recognized at the 100-m^2 scale and of four of those at the 0.1-m^2 scale. This winter/spring-wet stage seems to fit well with the *Eleocharis compressa-Schoenolierion croceum-Carex crawei-Allium cernuum* Herbaceous Vegetation Association of the *Eleocharis compressa-Nothoscordium bivalve* Saturated Herbaceous Alliance of NatureServe's (2005) International Vegetation Classification System. NatureServe (2005) also recognizes a *Dalea foliosa-Mecardonia-Mitreola petiolata* Herbaceous Association in thin soil along streams and a *Sedum pulchellum-Talinum calcaricum-Leavenworthia* spp./*Nostoc commune* (in depressions on limestone that hold water in winter and early spring) Association as wet community types on open glades in the Central Basin.

CONCLUDING REMARKS

We believe that the successional diagrams (Fig. 1, 2) will make it easier to comprehend the multiple starting points and pathways of succession in the middle Tennessee cedar glade vegetation complex, including how the various plant "associations" are related to each other. Further, these diagrams complement Quarterman's (1948, 1950a) detailed description of the apparent successional pathways in cedar glades (sensu lato) of the Central Basin of Tennessee, and they serve as a framework for other quantitative studies that have been (or will be) done on cedar glade vegetation in this physiographic region. Finally, they should be an aid to conservation planning in middle Tennessee, where human population growth and urbanization/industrialization is rapidly destroying much of the cedar glade habitat.

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